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Research Article

Acoustic analysis shows Clark's Nutcracker seasonal and spatial habitat use during post-fire recovery of two endangered pine species

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Abstract

Whitebark pine (*Pinus albicaulis*) and limber pine (*Pinus flexilis*) are endangered species in Alberta that rely on seed caching by Clark's Nutcracker (*Nucifraga columbiana*) for regeneration. Our objective was to determine which factors affect Clark's Nutcracker habitat use at the northern range limit of 5-needle pine co-occurrence, during fall foraging when seeds are cached, and during the following spring when seed caches are retrieved. This information is essential to inform recovery plans on potential for natural dispersal and regeneration on burns intended for 5-needle pine management. On a large, 2009 prescribed burn in Alberta (5600 ha), we used six automated acoustic recording devices from fall 2018 to spring 2020 to quantify Clark's Nutcracker habitat use. We tested whether Clark's Nutcracker habitat use differed between mast (2018) and non-mast years (2019), between whitebark and limber pine habitat, and burned versus unburned habitat. We used KALEIDOSCOPE PRO acoustic analysis software to quantify nutcracker calls from nearly 2000 hours of recordings with an advanced classifier. Model selection using Akaike's information criterion suggests that nutcracker habitat use depended on masting, habitat type, burned habitat, distance from seed sources, and one or more interactions, in both fall and spring foraging periods. Results from our study show that in the fall when both pine species produce high numbers of cones in close proximity, Clark's Nutcracker used whitebark pine habitat more, particularly unburned stands, suggesting more caching behavior. In the spring when seeds are retrieved, nutcracker habitat use was greater in the non-mast year, particularly in burned whitebark pine habitat. These habitat-use results suggest that in the 2018 mast year, both pine species benefitted from attracting seed dispersers, and further benefitted from lower habitat use the following spring, when caches are vulnerable to seed predation by nutcrackers. Whitebark pine attracted more nutcracker habitat use with fewer trees, and fewer cones per tree than limber pine. The 2009 prescribed burn created attractive habitat for Clark's nutcracker 9–11 years post-fire, demonstrating that opportunities for seed dispersal occur during this period. Continued use of trees resistant to white pine blister rust (*Cronartium ribicola*) by dispersers is essential for natural regeneration to be effective in current recovery strategies, and to leverage existing plantings of white pine blister rust resistant seedling as they reach cone production age in the future.

Key words: Acoustic analysis, Clark's Nutcracker, habitat use, limber pine, prescribed fire, restoration, seed dispersal, seed retrieval, whitebark pine

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Introduction

Limber pine (*Pinus flexilis*) and whitebark pine (*Pinus albicaulis*) rely on the Clark's Nutcracker (*Nucifraga columbiana*) in a mutualistic relationship for both seed dispersal and regeneration (Hutchins and Lanner 1982; Tomback and Linhart 1990; Windmuller-Campione and Long 2016; Ray et al. 2020). The co-evolved mutualism differs between the two pines with an obligatory relationship for whitebark pine (WBP), due to its indehiscent cones (Tomback 1982). Limber pine (LP) has a facultative relationship with nutcrackers, as the cones open upon maturity, allowing for gravity-based dispersal of wingless seeds (ASRD and ACA 2007a, 2007b). Both species depend on Clark's Nutcracker for long-distance seed dispersal (Lorenz et al. 2011) and gene flow (Tomback et al. 2001b; Jorgensen et al. 2002).

Nutcrackers exhibit behavioral flexibility, using both LP (Lanner and Vander Wall 1980; Vander Wall 1988) and WBP (Tomback 1983; Tomback 1998), as well as other conifer species in the Rocky Mountains (Lorenz et al. 2011; Schaming 2016; Clason 2017; Clason et al. 2020; Williams et al. 2020). Nutcrackers time fall seed caching activities according to dates of cone ripening, often shifting foraging activities along an elevational gradient to capitalize on mature cones (Tomback 1978; Williams et al. 2020). Cones mature in late August to September for limber pine (AWLPRT 2014) and mid-August to mid-September in whitebark pine (Tomback et al. 2001b). Quantitative and qualitative differences in nutcracker seed extraction, caching, and consumption behavior between LP and WBP will likely affect habitat use in montane (LP) vs. subalpine (WBP) habitat. Use of LP and WBP habitat may also differ in the spring, when nutcrackers retrieve seed to support themselves and offspring. Clark's Nutcracker exhibit remarkable memory of fall cache sites, retrieving caches through July of the following year (Tomback 1978; Schaming et al. 2024). The availability of remaining seed for regeneration of these species will be influenced by the allocation of time to both fall caching behavior and spring retrieval behavior. Habitat use as estimated by time spent in each habitat, will include a broader range of behaviors than foraging, including social interactions, predator avoidance, and nesting behavior.

Clark's Nutcracker show numerical responses at a regional level to cone crop size (Davis and Williams 1957; Davis and Williams 1964). Like many pines, both LP and WBP are masting species (Lanner and Vander Wall 1980; Lanner 1982; Tomback 1983; Tomback 1998), with large cone crops occurring every 2–4 years in LP (Peters et al. 2017), and every 3–5 years in WBP (Tomback et al. 2001b). Masting is evolutionarily advantageous as it attracts dispersers and promotes seed escape from predators (Janzen 1971; Kelly 1994), particularly red squirrels in the case of LP and WBP (McKinney and Fiedler 2009; Peters et al. 2017). Nutcrackers are responsive to interannual variation in cone crops and utilize cone crops in a probabilistic manner as cone density increases (McKinney et al. 2009; Barringer et al. 2012; Ray et al. 2020). Populations of birds using cone crops can reflect transient birds, as well as territorial birds (Lorenz et al. 2011). Nutcrackers exhibit optimal foraging behaviour in two key ways: their selection of 5-needle pine (species with 5-needle clusters borne on a short shoot), which have high caloric value, and selecting different masting species preferentially between years (Vander Wall 1988; Williams et al. 2020). Like other scatterhoarders, they commonly cache more seed (when available) than can be consumed (Tomback 1978; Vander Wall 2001). An overlooked component of Clark's Nutcracker

response to masting is in the spring following mast years, when caches are likely abundant despite granivory, and likely vary between conifer species. To our knowledge, only one study has documented spring retrieval in relation to WBP cone crops the preceding fall (Schaming 2016). Clark's Nutcracker have remarkable long-term memory of fall cache sites, retrieving seed in the field through July of the following year (Tomback 1978; Balda and Kamil 1992; Schaming et al. 2024); suggesting nutcrackers could show numerical responses in the spring following a mast year. Seed retrieval impacts seed availability and is a critical component of the regeneration process (Crawley 1997; Peters and Visscher 2019).

Detecting the presence and abundance of bird species is a critical task for conservation biologists, and recent advances in passive monitoring, through audio recording devices (ARD's), has become an increasingly important approach (Priyadarshani et al. 2018). Traditionally, acoustic monitoring effectively detects species through manual analysis of sound spectrograms, or listening by trained observers, or both. However, the labour-intensive nature of this task often limits the quantity of field recordings that can be analyzed (Taylor 1995; Wimmer et al. 2013). More recently, automated recognition of birdsong with advanced classifiers is allowing the rapid detection of individual bird species, across numerous sites and recording durations (Priyadarshani et al. 2018). Classifiers had not been reported for the detection of Clark's Nutcrackers at the time of our study, so we developed an advanced classifier using KALEIDOSCOPE PRO software (Wildlife Acoustics 2021) in this study to detect and record activity levels relative to year, habitat type, burn condition, distance, and fall caching versus spring seed retrieval periods.

Prescribed fire and wildfire are currently recommended as recovery strategies for restoring fire regimes of the endangered limber pine (provincial listing, Alberta) and endangered whitebark pine (provincial, and Canadian federal listing) (AEP 2022). Both species rely on the Clark's Nutcracker for seed dispersal (Tomback 1982; Tomback and Linhart 1990; Tomback et al. 2001b; Windmuller-Campion and Long 2016), and provincial recovery plans prioritize characterizing Clark's Nutcracker habitat use in areas supporting regeneration (AEP 2014). Dispersal of seeds by birds (zoochory) allows both pine species to disperse further, and at potentially greater densities, than wind-dispersed conifer species (Tomback and Linhart 1990; Willson 1993; Clark et al. 2005). Previous studies have shown that prescribed burns and wildfires provide suitable substrates for regeneration for both limber pine (Webster and Johnson 2000; Dawe et al. 2019) and whitebark pine (Moody 2006; Salvador 2018), and reduced competition, facilitating seedling growth and survivorship (Tomback et al. 1993; Tomback et al. 2001b; Coop and Schoettle 2009; Smith et al. 2011; Retzlaff et al. 2018). However, recent studies at the northern limit of limber pine and whitebark pine range overlap in Canada, are less clear on whether fire is equally necessary for both species. LP regeneration was virtually absent on 8–15-year-old fires but regenerated well in unburned stands (Dawe et al. 2019; Peters and Visscher 2019). WBP regenerated well on both prescribed burns and wildfires but achieved similar seedling densities in adjacent unburned stands (Salvador 2018). These findings raise obvious questions about whether Clark's Nutcracker prefer WBP versus LP habitat, and contributed directly to these differences, or whether differences in conditions for seed germination and survival contributed. There have been no studies in Canada that quantify nutcracker status or activity on burns (AWLPRT 2014; AEP 2022), or whether they use burned LP or WBP habitat more during either fall caching or spring seed retrieval periods.

We took advantage of a spatially expansive prescribed burn, which spanned both LP and WBP habitat, to investigate the role of spatial and temporal habitat characteristics on Clark's Nutcracker habitat use. The study burn in 2009 was intentionally prescribed to create regeneration opportunities for LP and WBP, following the release of the status reports for LP, and WBP, respectively (ASRD and ACA 2007a, 2007b), and concurrent provincial reviews for listing as endangered species (*pers. comm.*, ASRD and Alberta Whitebark and Limber Pine Working Group). The prescribed burn occurred at the northern limits of LP distribution in Kootenay Plains, Alberta, and is thus ecologically significant for assessing Clark's Nutcracker activity as a seed dispersal mutualist.

Our main question is what habitat characteristics are associated with Clark's Nutcracker habitat use. We then asked, if nutcrackers use WBP habitat more than LP habitat, and how this differs in burned vs. unburned habitat for each species. Cone supply varies interannually, and likely influences habitat selection for nutcrackers, so we asked whether habitat use differs between mast and non-mast years. We recognized that nutcrackers exhibit seasonal differences in foraging behavior, so we asked whether habitat use would differ between fall and spring periods. Our objective was to determine which factors affect habitat use by Clark's Nutcracker, and to explore habitat use in the context of the seasonal foraging behaviors of fall seed caching, and spring seed retrieval. We hypothesize that nutcrackers habitat use is influenced by one, or a combination of factors in habitat type (WBP vs. LP), burn condition (burned vs. unburned), distance into the burn, and timing (mast vs. non-mast year).

We predict that birds use 5-needle pine habitat more in mast versus non-mast years in fall when seeds are cached, and also use 5-needle pine habitat more in the spring when seed caches are retrieved following mast years, than in springs following non-mast years. We further predict that Clark's Nutcracker use burned WBP habitat more than burned LP habitat during fall caching, due to greater observed seedling regeneration in burned WBP habitat in northern prescribed burns and wildfires. Quantifying Clark's Nutcracker presence and habitat use during foraging periods provides the first step in answering basic behavioral questions related to habitat use, and understanding the role of bird-mediated seed dispersal in the regeneration process of LP and WBP. Currently, there is no documentation of Clark's Nutcracker habitat use of prescribed burns or wildfires in Canada, limiting our knowledge of the efficacy of fire as a recovery strategy for bird-assisted regeneration of both the endangered LP and WBP.

Methods

Study area

The study location was at the northern limits of LP range in North America, on the 2009 Upper North Saskatchewan Prescribed Burn near Abraham Lake, Alberta (52.03°N, 116.60°W (DMS)) (Fig. 1a). The burn was chosen because it is the only known historic fire in Alberta with both LP and WBP populations within the burn perimeter, and immediately adjacent to it. The burn spans both montane habitat with LP in the valley bottom to midslope (1426 m–1750 m), and extends to the subalpine habitat with WBP (elevation 1800–2250 m). It thus provides comparisons of foraging preferences on burns where both species are with-

in observed daily movement flights of nutcrackers (*pers. obs.*). The prescribed burn was approximately 5600 ha in size and is easily accessed via the Landslide Lake Interpretive Fire Trail. The spring burn prescription led to a high-severity fire, with 100% tree mortality in most stands, with variable duff consumption, and mineral soil exposure, and are presented in more detail for WBP habitat in Salvador (2018), and LP habitat in Dawe et al. (2019). Stands of burned and unburned WBP line the upper fire edge. Pockets of LP are found along ridges, within the burn, and along the adjacent banks of the North Saskatchewan River, with a substantive unburned stand (~388 ha) bordering the eastern side of the burn. These stands serve as a seed source site for nutcracker activity and seed dispersal. Prior studies have confirmed the occurrence of post-fire regeneration, of predominantly WBP seedlings (Salvador 2018; Dawe et al. 2019), raising questions of whether nutcrackers were preferentially selecting WBP cone resources, and WBP habitat for caching, on both the study burn, and other burns where both pine species are within the dispersal limits of nutcrackers.

Cone surveys and stand characterization

We observed high numbers of cones in 2018 at nine historic northern cone monitoring sites (Fig. 1a), which enabled us to initiate a mast year comparison study starting in 2018. Both WBP and LP show understory regeneration in open mature stands, and both immediate and ongoing regeneration following fire, so we made the assumption that Clark's Nutcracker activity on a 9-year-old burn would capture activity in relation to habitat characteristics that would contribute to future regeneration for both species. We annually monitored 10 tagged trees in each year from 2018 to 2020 in both a LP stand and a WBP stand, each situated in the burn perimeter (Fig. 1b). We confirmed that 2018 was a LP mast crop by comparing the same 10 LP trees in the burn perimeter to their cones counts in 2008–2010, and to 680 trees, that were monitored across 17 stands spanning the range of LP in Alberta (Peters et al. 2017). Cones were observed in WBP in 2018, but we did not have earlier records to compare cone production to (Table 1). We characterized stand composition along a 200 m transect extending from the burn perimeter into the unburned seed source. The basal area of each tree species was calculated from a basal area factor (BAF 2 m) prism count at 50 m intervals along this transect (Fig. 1b).

Acoustic survey

To quantify nutcracker habitat use relative to cone crops and habitat types, audio recording devices (ARD's) were maintained between 2018–2020, within and adjacent to the ~5600 ha burn. To separate habitat use by the treatments of mast vs. non-mast year, pine species, burned vs. unburned habitat, and distance into the burn, six ARD's were placed along an elevational gradient adjacent to existing stands of LP or WBP (Fig. 1b). For each stand type, a single ARD was set up at 0 m, 500 m, and 1000 m into the burn (at 1456 m, 1666 m, and 1747 m elevation, for LP, and 2173 m, 2075 m, and 1899 m respectively, for WBP). The unburned stand acted as the control environment for this field study, and was situated 100 m from the edge of the burn (hence referred to as the 0 m site). ARD's were attached 1.5 m above the base of tree trunks to avoid

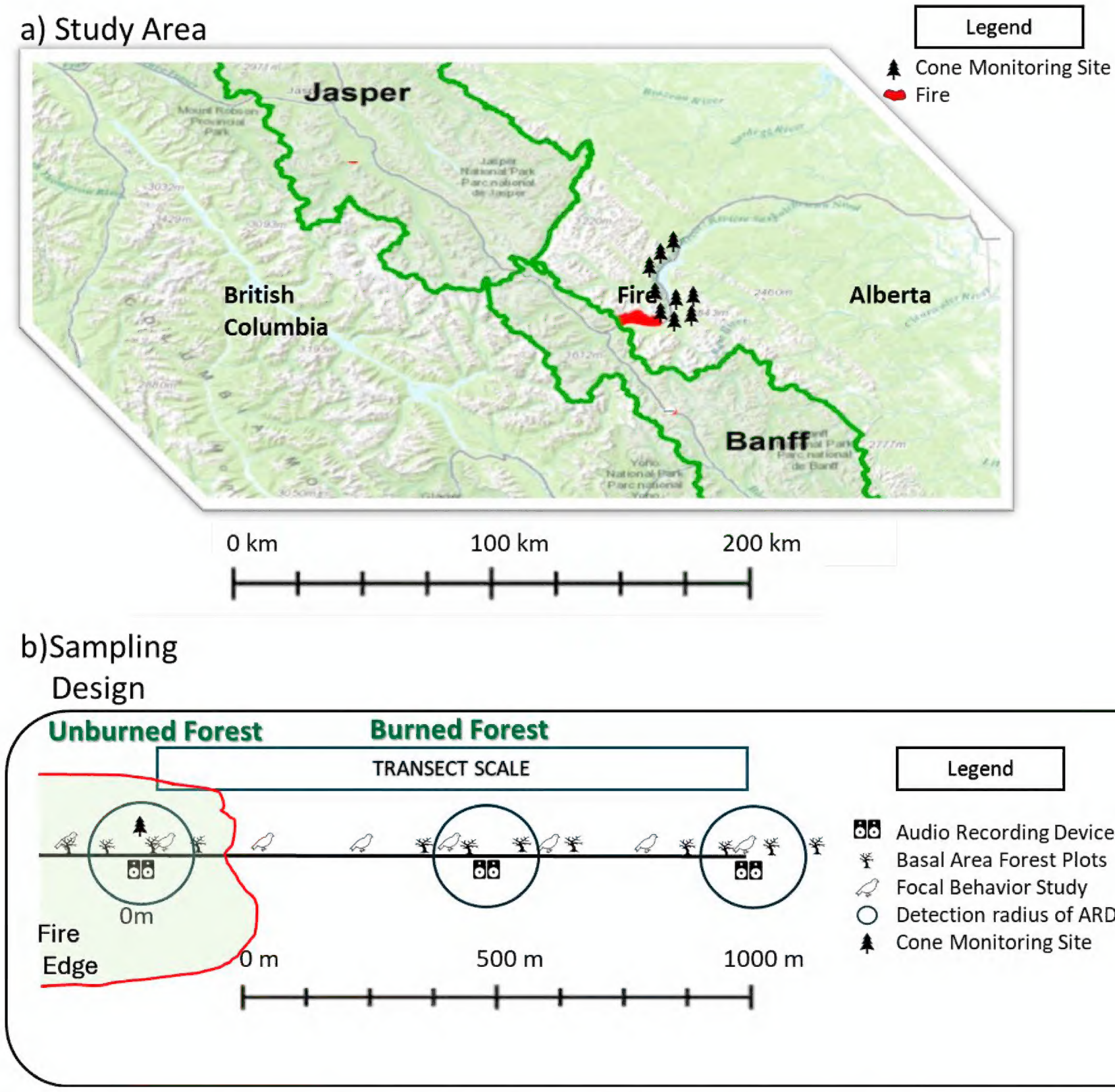

Figure 1. a. Map showing the location of 2009 study fire and nine historic cone monitoring sites in Alberta from the northern portion of the species range; **b.** The above sampling design was repeated in both whitebark pine habitat, and limber pine habitat. It shows the location of audio recording devices in burned and unburned stands and the assumed detection distances of calling nutcrackers. The location of point counts for focal behavior studies of nutcrackers is shown, as well as cone monitoring plots for the current study, and forest composition plots that were sampled for basal area of tree species.

sound interference with branches and foliage. ARD's recorded in studio, and included four SongMeter 1 units, and two SongMeter 2 units, manufactured by Wildlife Acoustics. All SongMeter 1 units were calibrated to have equal microphone sensitivity and to be within an acceptable range of the SongMeter 2 units (< 3%). Units were deployed randomly between sites each season and year, so the model type would not impact the overall result of the study.

The ARD's recorded the fall caching season for the 2018 mast year and the 2019 non-mast year. Audio was recorded from August 8 to August 24, which was a period that attempted to ensure seed availability in both species, that counterbalanced: 1) high predation rates by squirrels at this time in LP (Peters et al. 2017), and WBP (Leslie and Wilson 2011), 2) reported dates of seed release in LP in AB, (Aug. 25th, Langor, pers comm), and 3) the northernmost reports of both LP and WBP pouching, foraging, or caching by Clark's Nutcracker in the literature (Aug 26th, Vander Wall 1988); and WBP (early July (Leslie and

Table 1. Annual cone production estimates and forest parameters in unburned (0 m) seed sources (+/- 1 SE).

Forest type	Cones/tree by year			Forest composition Basal area/species (m^2/ha)		
Pinus flexilis	**2018**	**2019**	**2020**	***Pinus flexilis***	***Pinus contorta***	***Picea glauca***
	155.6+/-28.8	0.0	11.6+/-3.0	2.3+/-0.46	0.1+/-0.1	0.2+/-0.1
Pinus albicaulis	**2018**	**2019**	**2020**	***Pinus albicaulis***	***Pinus contorta***	***Abies lasiocarpa***
	12.0+/-5.4	0.0	0.0	0.2+/- 0.2	1.4+/- 0.75	0.8+/-0.37

Wilson 2011) to mid August (Scott 2013; Schaming et al. 2024)). Nutcrackers can feed on immature WBP cones (Ray et al. 2020), so these dates assess foraging activity across both species. To quantify interannual effects of masting on nutcracker seed retrieval, activity was monitored in the spring following the mast year (2019) and non-mast year (2020), respectively, once > 50% of ground substrates were exposed in WBP stands (from May 21 – June 6). Within these periods, 17 days of audio was recorded at 7–9 am, 12–1 pm, and 3–5 pm for a total of five hours each day. Recording periods were treated as independent replicates to assess activity (3 per day; with a minimum of 51 recording periods/fall or spring season), because individual nutcrackers are capable of long-distance seed dispersal (up to 33 km (Lorenz et al. 2011)) between foraging and caching sites each day. Their mobility allowed local birds to leave a recording site, and visit the same, or other sites, in separate recording periods, and also allowed new birds to arrive from off site between recording intervals. Foraging groups were routinely seen flying between sites, several times per day (pers. obs.), suggesting birds did not stay longer at a site once there, and temporal and spatial autocorrelation analyses would not be important biologically, compared to habitat selection. All recordings were standardized to calls/hour, to account for longer subsamples per recording period in morning and mid-afternoon recording periods. Overall, ARD's were set up to monitor seasonal foraging behavior relative to cone crop, LP vs. WBP habitat, distance into the burn site, and time of day.

Acoustic analysis

Recorded audio was analyzed in KALEIDOSCOPE PRO software (Wildlife Acoustics 2021) using the Basic Cluster Analysis and Advanced Classifier tools. This program is used to scan audio recordings for specific sounds using inputted parameters (Pérez-Granados and Schuchmann 2020). The parameters included: minimum and maximum frequency range in Hz, minimum and maximum length of detection in seconds, and maximum inter-syllable gap in seconds. The goal was to use a set of parameters that allowed the program to detect the highest number of nutcracker calls while minimizing false positives (described below). Nutcrackers make a wide variety of vocalizations, reflecting 13 types of calls (Tomback in Schaming et al. 2024). We quantified the frequency of call types in our training dataset, to understand which calls our acoustic analyses were most sensitive to. We did not attempt to distinguish between types of calls in the overall analysis, or between individuals, and recognize that these are important avenues of research for other studies focusing on either behavior in relation to call types, or quantifying the abundance of nutcrackers.

Datasets from four different recording periods were analyzed in KALEIDOSCOPE PRO for the number of nutcracker calls. The datasets were: Fall 2018, Spring 2019, Fall 2019 and Spring 2020. Audio Recording Units were active at three intervals throughout the day during these recording periods, from 7–9 am, 12–1 pm, and 3–5 pm. Prior to analysis in KALEIDOSCOPE PRO, a human observer audibly scanned all recordings for noise using RAVENPRO 1.6 software (The Cornell Lab of Ornithology 2026) that would make the nutcracker call indetectable by KALEIDOSCOPE PRO. We removed files from the dataset if a human observer determined that at least 20% of the recording was inaudible because of interference from wind, rain, or other disturbances, a procedure used in other studies (Buxton et al. 2016). For the fall and spring datasets, 38.55% and 38.60% of the recordings, respectively, were omitted due to at least 20% of the recording being inaudible. The percentage of removed recordings for each audio recording device were tested statistically to ensure a similar number of usable recordings were associated with individual ARD's, and factors tested in our study.

Basic cluster analysis

A basic cluster analysis was performed in KALEIDOSCOPE PRO, using the following set of parameters: 2000–2300 Hz for minimum and maximum frequency range, 0.2–10 s for minimum and maximum length of detection, and a 0.001 s maximum inter-syllable gap. We trained the program with an Aug. 9, 2019 recording (7–9 AM), in WBP habitat, 1000 m into the burn. It was selected because it contained several types of nutcracker calls, had no background noise from wind or rain, detected 99.2% of calls correctly (0.8% false positives), and did not miss a single nutcracker call (100% detection rate, n = 134 calls). This recording was run through a basic cluster analysis, after which we listened to all the calls that KALEIDOSCOPE PRO detected and manually selected which ones were in fact, Clark's Nutcracker calls, and which ones were not.

Advanced classifier

Using the results of the basic cluster analysis, we created an advanced classifier. The same Aug. 9th recording was run through a second cluster analysis, and manual selection of nutcracker calls was used to further train the classifier. We processed separate batches of audio files from each of the four recording periods (Fall 2018, Spring 2019, Fall 2019 and Spring 2020) with the advanced classifier to detect nutcracker calls. An observer manually quantified the frequency of nutcracker call types in the Aug. 9th training recording using the 13 vocalization types described by Schaming et al. (2024). Three call types were identified in this recording based on comparisons to sample recordings, with alarm calls predominating (52.5%), followed by slow and fast locational calls (25.2 and 12.8%, respectively), while shrill/mew calls (9.5%) were identified based on verbal descriptions of the call. The accuracy of call detection with the advanced classifier in KALEIDOSCOPE PRO was compared to manual detection with RAVENPRO. This validation procedure included comparisons of seven additional recordings that were randomly selected from all six ARU's, spanning LP and WBP habitat, from all fall recordings (2018 and 2019), to the Aug. 9th, 2019 training file, which was reported in the basic cluster analysis methods.

Detection rates averaged 44.5%, and false detection rates averaged 22.3%, and either met or exceeded the ROC curve for a "good" auto detector (Charif et al. 2010). By removing the recordings with sound interference from our data analysis, we increased the precision of the advanced classifier, by limiting false positives, and improved recall by reducing false negatives.

Activity metrics

The calls detected for each recording were standardized to "calls per hour" and referred to as vocal activity rate (VAR). Vocal activity rate is commonly used to assess relative activity of birds from ARU data (Pérez-Granados and Traba 2021), and measures of Clark's Nutcracker vocalization activity have been successfully used to determine their habitat use in relation to WBP stand characteristics (Kovalenko et al. 2024). In this study, VAR measures Clark's Nutcracker presence in a habitat, and we interpret presence as indicative of habitat use. The terms VAR and habitat use will be used from here forward. Several methods were used to ensure both the consistency of activity metrics, as well as the quality of automated data collection. Firstly, the analysis in KALEIDOSCOPE PRO removed observer differences that occurred when manual detection of calls was performed solely using RAVENPRO software (The Cornell Lab of Ornithology 2026). Missed calls (false negatives) were often quiet calls, or distant birds, that can only be manually detected through visual observation in RAVENPRO. To independently verify that KALEIDOSCOPE PRO output was reflective of differences in calling, we quantified the number of call bursts (defined as continuous calls with less than 10 s gap between calls), and total calling time from actual bird spectrograms in RAVENPRO. Data from all ARU's, from the entire mast and non-mast years period recorded earlier were used.

Focal behavior studies

We conducted a pilot study of point counts and focal behavior studies (FBS) to assess nutcracker behavior during caching and seed retrieval periods in the fall (Aug 5–6, 2020) and spring (June 3–5, 2021 for both habitats, and June 26, for upper elevation WBP habitat). Behavior data lends some support to whether caching or seed retrieval occurred by individual nutcrackers while other flock members were vocalizing. Ten point-counts were conducted along a 2 km transect in both LP habitat, and WBP habitat, respectively, and sampled both unburned and burned habitat (Fig. 1b). Point counts were for 10-minute durations, and occurred at 200 m intervals (we assumed a 100 m detection radius) within habitats until nutcrackers were located. We then approached a bird (20–30 m) and documented all behaviors for up to a 10-minute interval, provided the bird remained visible with binoculars (8× magnification), and then switched our attention to the next nearest bird, for additional FBS counts. We documented the number of birds present, and for our focal birds, the duration of calling, and duration of all non-foraging activities (flying, perching, preening), and foraging activities (caching or retrieving). The number of FBS depended on encountering calling nutcrackers during point counts. During the fall caching period, a total of 7 FBS were conducted in LP habitat, and 1 FBS in WBP habitat, while during the spring retrieval period, 22 FBS were conducted in

LP habitat, and 7 in WBP habitat. Inclement weather occurred on the days we sampled WBP habitat and did not allow for equitable nutcracker detection and FBS in both habitats or periods.

Statistical analysis

All statistical analyses were performed using R version 4.0.2 (R Core Team 2018). We tested specific ecological factors that we hypothesized would influence nutcracker activity using a generalized linear model (GLM) approach to fit models of detected calls. Clark's Nutcracker vocal activity rate was used as the response variable to assess "presence", which we interpret as reflective of "habitat use". Model factors were not correlated, and thus all four factors were included, as shown in Table 2. These variables were mast versus non-mast years, LP versus WBP habitat, burned versus unburned habitat, and distance into burned habitat (the unburned site was assigned as 0 m, rather than 100, for statistical purposes). We treated time periods as independent and therefore analyzed data by time period in separate models for the fall seed-caching period and the spring seed-retrieval period, as VAR during these periods may be influenced by different ecological factors.

Model identification

To determine the most appropriate distribution using a GLM framework, we compared the AIC results of saturated models from the fall and spring datasets using both a Poisson and a negative binomial distribution. Nutcrackers were detected in most recordings at low VAR, and the VAR distribution was right skewed with a few very high VAR, so we tested whether the Poisson or negative binomial model form was valid. A negative binomial distribution was selected for model generation for both the spring and fall analysis, based on a comparison of Akaike's Information Criterion (AIC values). Additionally, our saturated models indicated there was overdispersion, which the negative binomial distribution allows (Zuur et al. 2010; Linden and Mantyniemi 2011). We specified the negative binomial distribution using the MASS package in R, using the code "glm.nb" for the model (R Core Team 2018).

Table 2. *A priori* hypotheses (models) and their respective factor and factor descriptions. We hypothesize that nutcracker habitat use is influenced by one or a combination of the factors described here.

Hypothesis name	Reason	Factor	Description
Timing of Masting	Nutcracker habitat use is hypothesized to be higher in mast versus non-mast years due to greater seed availability	Mast	Mast year was fall 2018 – spring 2019, and non-mast year was fall 2019 – spring 2020
Habitat Type	WBP is hypothesized to be used more during caching periods, and used less during retrieval periods because it is regenerating better than LP†	Habitat	3 sites in LP habitat, 3 sites in WBP habitat
Burn Condition	Nutcrackers may preferentially cache and/or retrieve seeds in disturbed sites (burned vs. unburned sites)	Burn	Previously burned area from the 2009 Upper Saskatchewan Fire, versus unburned area
Distance	Nutcrackers may cache/retrieve seeds preferentially in unburned habitat versus the burn to minimize foraging costs	Distance	Sites at: 0 m, 500 m, and 1000 m into the burn for both LP and WBP (0 m is unburned habitat)

† LP is limber pine, while WBP is whitebark pine.

Model generation and selection

We used Akaike's Information Criterion (AIC) to determine which model was the most parsimonious for explaining nutcracker activity from our *a priori* candidate model set, and interactions of factors (Table 2; Akaike 1973; Burnham and Anderson 2002). After identifying the top candidate model (a saturated model with all factors and interactions between mast year and habitat type, and habitat type and burned condition), we inspected model residuals to confirm that errors were homogenous and independent with respect to model factors. Models in the candidate set for both the fall and spring were analyzed for parsimony using AIC, log likelihood values, and model weight, and significance using p-value (Tables 3, 4).

A two-sample t-test assuming equal variance (one-tail) compared mast crop size between the 2010 and 2018 mast years. We performed a series of chi-square tests to examine the potential influence of weather on the number of usable (good weather) recordings versus the number of omitted recordings (bad weather) across the six recording sites. This test was performed on the fall data set, and spring data set, and each factor identified in the GLM analyses, namely masting, habitat type, burned condition, and distance into the burn were tested to see if they were disproportionately affected by the removal of poor quality recordings. Linear regressions were performed on fall caching time and spring seed retrieval time relative to calling time in each habitat for birds observed in focal behavior studies.

Results

Factors affecting fall nutcracker habitat use

Model selection using AIC suggests strong support for modelling Clark's Nutcracker VAR as a function of all seasonal and habitat factors tested (mast vs. non-mast year, LP vs. WBP habitat, burned versus unburned habitat, distance into the burn); the saturated model was most parsimonious (ΔAIC = 13.742, wi = 0.999). It contained factors from each of the *a priori* hypotheses, as well as interactions between mast years and habitat type, and burns versus habitat type (Table 3). All factors and interactions in the saturated model contributed significantly ($p < 0.001$, respectively; Table 4). In fall, inclement weather reduced the number of recordings included in the above analyses, but did not affect the number of recordings removed between any of the factors compared in models (i.e. mast vs. non-mast years (x^2 (1, 159) = 0.183, p = 0.669), habitat type (x^2 (5, 601) = 2.402, p = 0.121), burned condition (x^2 (5, 601) = 0.6592, p = 0.883), or distance into the burn (x^2 (5, 601) = 1.929, p = 0.859).

Timing of masting and cone availability

2018 was a mast year for the LP stand adjacent to the study burn, with a mean of 155.8 cones/tree, while 2019 was a cone failure year, and 2020 was a low cone production year (Table 1). Limber pine cone production in 2018 was 1.9 times greater than the 2010 mast year at the same site (t = 3.85; p = 0.0007).

Table 3. Model selection results from candidate models for nutcracker activity during fall and spring recording periods.

Hypothesis	Fall caching					Spring retrieval			
	K	LL	AIC	ΔAIC	Wi	LL	AIC	ΔAIC	Wi
VAR | M+H+B+D+M*H+B*H†	7	-1500.9	3017.8	0	0.999	-1556.2	3128.4	0	0.999
VAR | M+H+B+D	5	-1509.8	3031.6	13.7	0.001	-1586.9	3185.8	57.4	< 0.001
VAR | M*H+B*H	3	-1516.1	3046.1	28.3	<0.001	-1567.4	3148.8	20.3	< 0.001
VAR | M*H	2	-1533.3	3076.5	58.7	<0.001	-1597.3	3204.7	76.2	< 0.001
VAR | H+B+D+B*H	5	-1543.2	3098.4	80.5	<0.001	-1573.9	3159.9	31.4	< 0.001
VAR | M+B+D	4	-1551.1	3112.3	94.5	<0.001	‡			
VAR | H*B	2	-1558.9	3127.7	109.9	<0.001	-1589.1	3188.3	59.8	< 0.001
VAR | M	2	-1565.7	3137.3	119.4	<0.001	-1676.6	3359.2	230.8	< 0.001
VAR | H+D	3	-1568.9	3145.7	127. 9	<0.001	‡			
VAR | H	2	-1570.6	3147.1	129.3	<0.001	-1611.6	3229.3	100.8	< 0.001
VAR | B	2	-1581.7	3169.4	151.6	<0.001	-1691.1	3388.2	259.8	< 0.001
VAR | D	2	-1587.2	3180.5	162.6	<0.001	-1686.6	3379.2	259.8	< 0.001

Notes: All models are general linear models with a negative binomial distribution. Bold text indicates the top model of those evaluated per Akaike weight. Models are listed in decreasing rank, with number of estimated parameters (K), values for log-likelihood (LL), Akaike's Information Criterion (AIC), difference in AIC (ΔAIC), and model weight (Wi). Models are in the format of response variable | independent variables, where nutcracker calls/h is vocal activity rate (VAR), timing of masting is indicated by (M), limber pine versus whitebark pine habitat type is (H), burned versus unburned condition is (B), and distance into the burn is (D).
†Henceforth referred to as the "saturated model" for both fall caching and spring retrieval.
‡We used backwards stepwise selection to sequentially remove the least statistically significant variable in models, based on p-value, resulting in fewer models (Addi et al. 2021).

Table 4. Factors tested and the coefficient of the fixed effect in the most parsimonious fall and spring model (Table 3).

Factor	Fall caching			Spring dispersal		
Fixed Effects	Coefficient Estimate	SE	*p*	Coefficient Estimate	SE	*p*
Timing of Masting	1.437	0.172	<0.001	-0.594	0.195	0.002
Habitat Type	0.904	0.235	<0.001	0.864	0.246	<0.001
Burn Condition	-2.333	0.28	<0.001	-2.76	0.326	<0.001
Distance into Burn	0.002	0.0003	<0.001	0.0016	0.0003	<0.001
Masting* Habitat Type	-0.468	0.237	0.0484	-0.415	0.262	0.114
Habitat Type* Burned Condition	0.914	0.242	<0.001	2.147	0.271	<0.001

The standard error of the estimate (SE) and significance (p) are given. In total there were 102 recording periods (51/year) at sites in the fall model, and 133 recording periods (51 in 2019, and 82 in 2020) at sites in the spring model, respectively.

In 2018, WBP had the highest cone production observed over the 3-year study period (12 cones/tree, versus no cones in 2019, and 2020, respectively; Table 1). Clark's Nutcracker vocal activity during the seasonal peak of mature seed availability of these species was 1.6 times greater in the mast year (42.4 calls/h), than the same sites in the non-mast year (16.4 calls/h), the following fall (2019; Fig. 2a, b), when cone crops failed, and no cones were observed in either LP and WBP. Independent analysis of call bursts/h and total calling time/h supported these findings, with 0.27 times and 0.34 times greater calling, respectively, in mast years. On the other hand, the number of days on which nutcrackers were detected was virtually the same in mast and non-mast years (100% of days at the same four ARU's (LP 0 m, WBP 0 m, WBP 500 m, and WBP 1000 m), respectively), and a mean of 72.5% in the remaining two ARU's (LP 500 m and LP 1000 m) vs. 74% of days in mast vs. non-mast years, respectively.

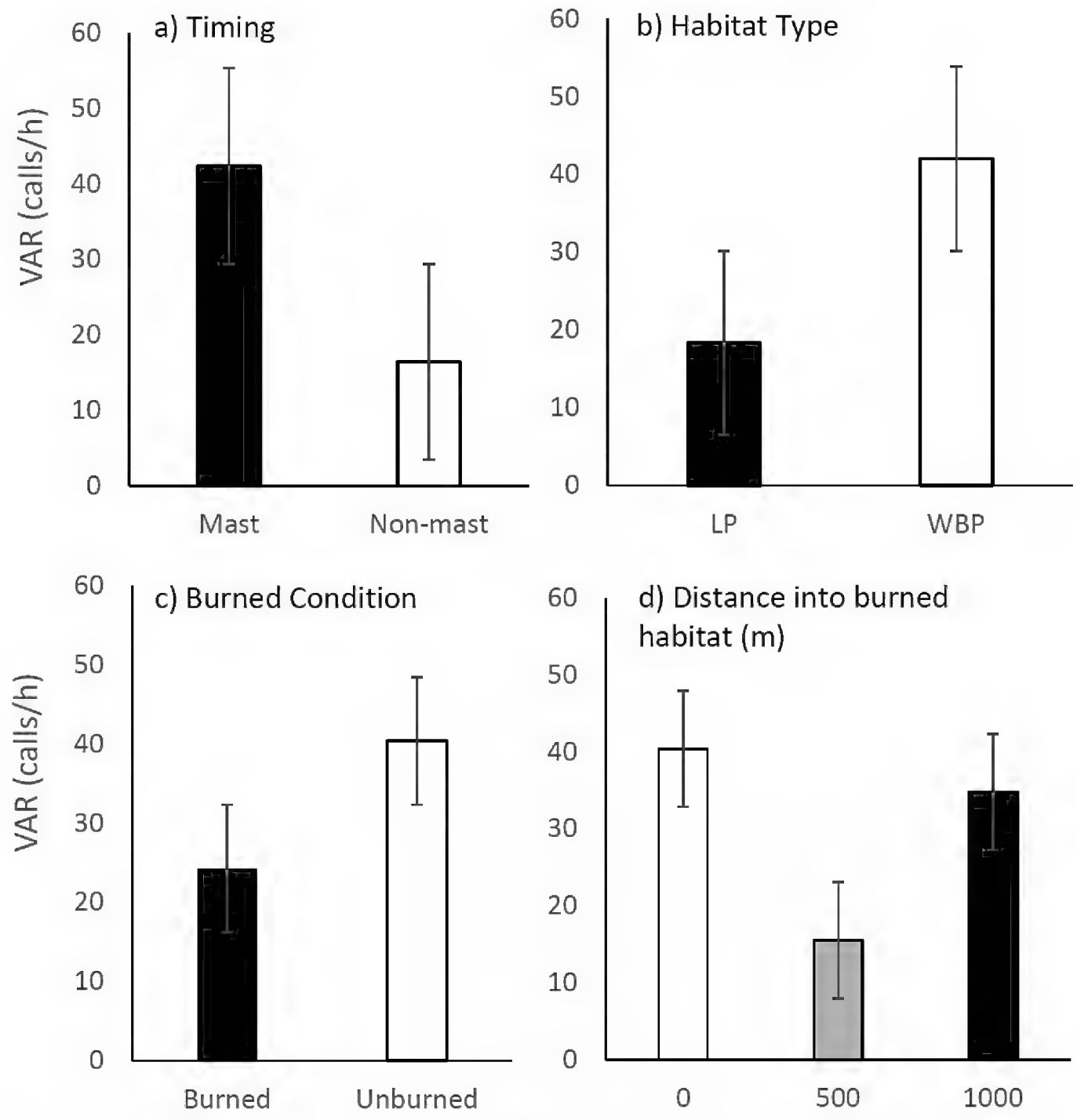

Figure 2. Nutcracker vocal activity rate (VAR) in the fall relative to seed availability and habitat factors. VAR is average calls per hour (h) and is shown relative to: **a.** Mast versus non-mast year (n = 6 automatic recording units (ARU's), respectively); **b.** Limber pine (LP) versus whitebark pine (WBP) habitat (n = 3 ARU's, respectively); **c.** Burned versus unburned habitat (n = 4 and 2, ARU's, respectively); **d.** Distance into burned habitat (n = 2, ARU's, respectively). Standard error bars are shown (+/- 1 SE).

Habitat use

Clark's Nutcracker vocal activity (calls/h) in the fall was 1.3 times greater overall in WBP habitat, than LP habitat (Fig. 3b). Nutcracker habitat use was 0.70 times greater in unburned seed sources (0 m), than burned habitat (Fig. 2c); interestingly, habitat use was nearly as high 1000 m into the burn as in unburned seed sources (Fig. 2d). Masting affected fall habitat use, with proportionately higher use of LP in mast years vs. non-mast years than in WBP mast years vs. non-mast years (3.0 vs. 1.7 times greater, respectively; Fig. 3, Interaction I). Habitat type affected the use of burns, with proportionately higher nutcracker use of burned WBP vs burned LP (1.9 times greater; Fig. 3, Interaction II). There was some preference for unburned WBP seed sources vs. unburned LP (0.9 times greater; Fig. 3, Interaction II). Overall, nutcrackers were detected in 81.7% days in LP habitat vs. 100% in WBP habitat (three ARU's, respectively); in 86.3% days in burned vs. 100% days in unburned habitat (four vs. two ARU's, respectively); and 100% days at 0 m, 85.5% days at 500 m and 100% days at 1000 m into the burn (two ARU's, respectively, in all cases).

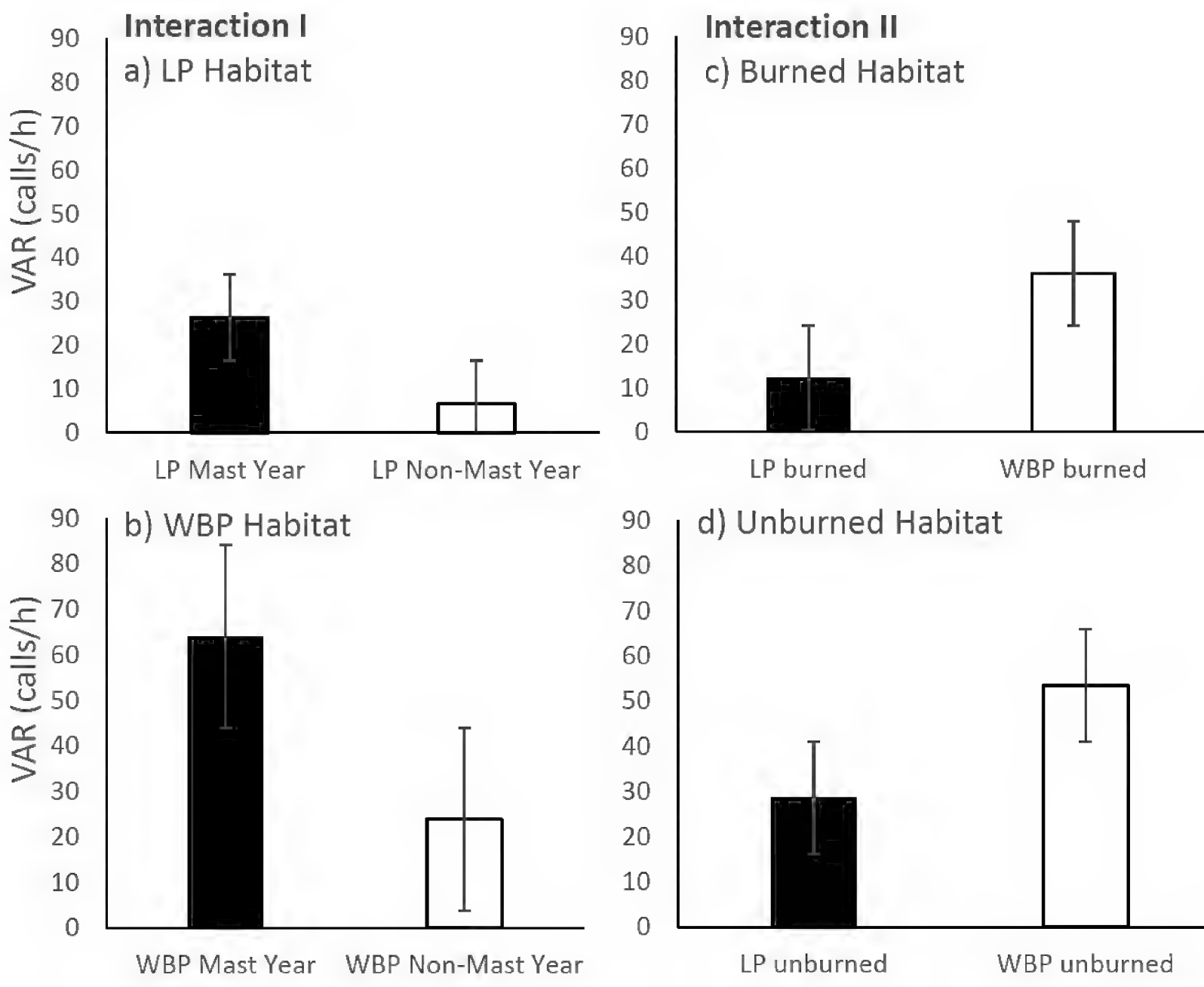

Figure 3. Nutcracker vocal activity rate (VAR) in the fall relative to habitat and seed availability interactions. VAR is average nutcracker calls per hour (h) and is depicted relative to interaction I, between habitat type (limber pine (LP) and whitebark pine (WBP)), and timing of mast vs. non-mast year, and interaction II, between burn condition and habitat type (+/- 1 SE).

Factors affecting spring habitat use

Model selection using AIC suggests strong support for modelling spring Clark's Nutcracker VAR as a function of all seasonal and habitat factors tested (mast vs. non-mast year, LP vs. WBP habitat, burned versus unburned habitat, distance into the burn) and including two-way interactions between mast year and habitat type, and habitat type and burn condition. Thus, spring model selection suggested that there was the most evidence for the saturated model (ΔAIC = 20.346, wi = 0.999, Table 3). The saturated model showed us that less VAR occurs on mast years in the spring than non-mast years, that WBP habitat was used more than LP habitat, that burned habitat was used more than unburned habitat, and that there was an increase in VAR with distance into the burn ($p < 0.001$, in all cases respectively; Table 4). The effect of the mast year and habitat type interaction changed from the fall analysis, and had a negative effect in the spring analysis, but was not significant ($p = 0.114$; Table 4). Inclement weather reduced the number of recordings included in the above analyses, but did not affect the number of recordings removed between any of the factors compared in models (i.e. mast vs. non-mast years (x^2 (1, 227) = 0.059, p = 0.808), habitat type (x^2 (5, 798) = 0.026, p = 0.0872), burned condition (x^2 (5, 798) = 0.977, p = 0.807), or distance into the burn (χ^2 (5, 798) = 4.4118, p = 0.492).

Timing of masting and seed availability

Despite the likely availability of cached seed from high levels of habitat use by Clark's Nutcracker during the fall of 2018 mast crop, nutcracker VAR was significantly lower the following spring (2019), with only 0.4 times the vocal activity in 2019, than occurred in 2020, following a low cone crop (Fig. 4a; $p = 0.002$). In the mast year spring (2019), nutcrackers were encountered 100% of days at four of the ARU's (LP 0 m, WBP 0 m, WBP 500 m, and WBP 1000 m), and 53% and 47% of days at LP 500 m and LP 1000 m, respectively (n = 6 ARU's). In the non-mast year, nutcrackers were detected in 100% of days at the same four ARU's, and in 85% and 69% of days at LP 500 m and LP 1000 m, respectively (n = 6 ARU's).

Habitat use

Spring habitat use was 7.1 times greater in WBP habitat than in LP habitat (Fig. 4b). Nutcracker habitat use in the spring was greater in the burn site at 1000 m than the unburned seed source (0.9 times more vocal activity occurred than in the unburned seed sources (Fig. 4d)). Habitat use was higher in the non-mast year in WBP, but not in LP habitat ($p < 0.001$; Fig. 5; Interaction I). Spring habitat use was 0.25 times greater in burned habitat than unburned habitat, but differed between habitat type, where in burned WBP habitat, it was used 15.7 times more than burned LP habitat (Fig. 5; Interaction II). Unburned WBP habitat was used only 1.6 times more than LP habitat (Fig. 5, Interaction II). Overall, nutcrackers were detected in spring in 100%, 68% and 58% of days at LP 0 m, LP 500 m and LP 1000 m, respectively, vs. 100% of days at all three WBP ARU's. Nutcrackers were detected in 100% of days in unburned habitat for LP and WBP respectively, 100% of days in burned WBP habitat, but only 63% of days in burned LP habitat (n = 2 ARU's, in all cases). This data helped explain the lower use of LP habitat in the spring, particularly in the burn (Figs 4b, 5c, respectively).

Focal behavior studies

Nutcrackers were consistently engaged in active foraging behaviors in fall and spring periods when calling activity occurred, and birds were using LP and WBP habitat. Birds that were actively foraging were typically quiet, while other birds in the same group were typically calling intermittently, while perched in nearby trees. During the fall seed caching period, the ratio of foraging minutes to calling minutes was 1.1 times greater compared to the spring seed retrieval period (0.85 vs. 0.40, respectively). (Appendix 1). In the spring, we did not see differences in the foraging to calling time ratio between LP habitat vs. WBP habitat (0.43 vs. 0.37, respectively). The mean number of birds encountered in groups during focal behavior studies was also similar between LP and WBP habitat (n = 2.5 vs. 2.6; unpublished data) in the spring, which was the only period we had substantial data for both habitats (Appendix 1). These results show that although calling is associated with both caching and seed retrieval, we did not detect a significant relationship in either habitat type between length of calling time, and the time spent caching or seed retrieving in FBS ($r^2 < 0.51$, $p < 0.32$, in all cases). Inclement weather limited FBS in WBP habitat in the fall, and likely inhibited calling in the one FBS completed.

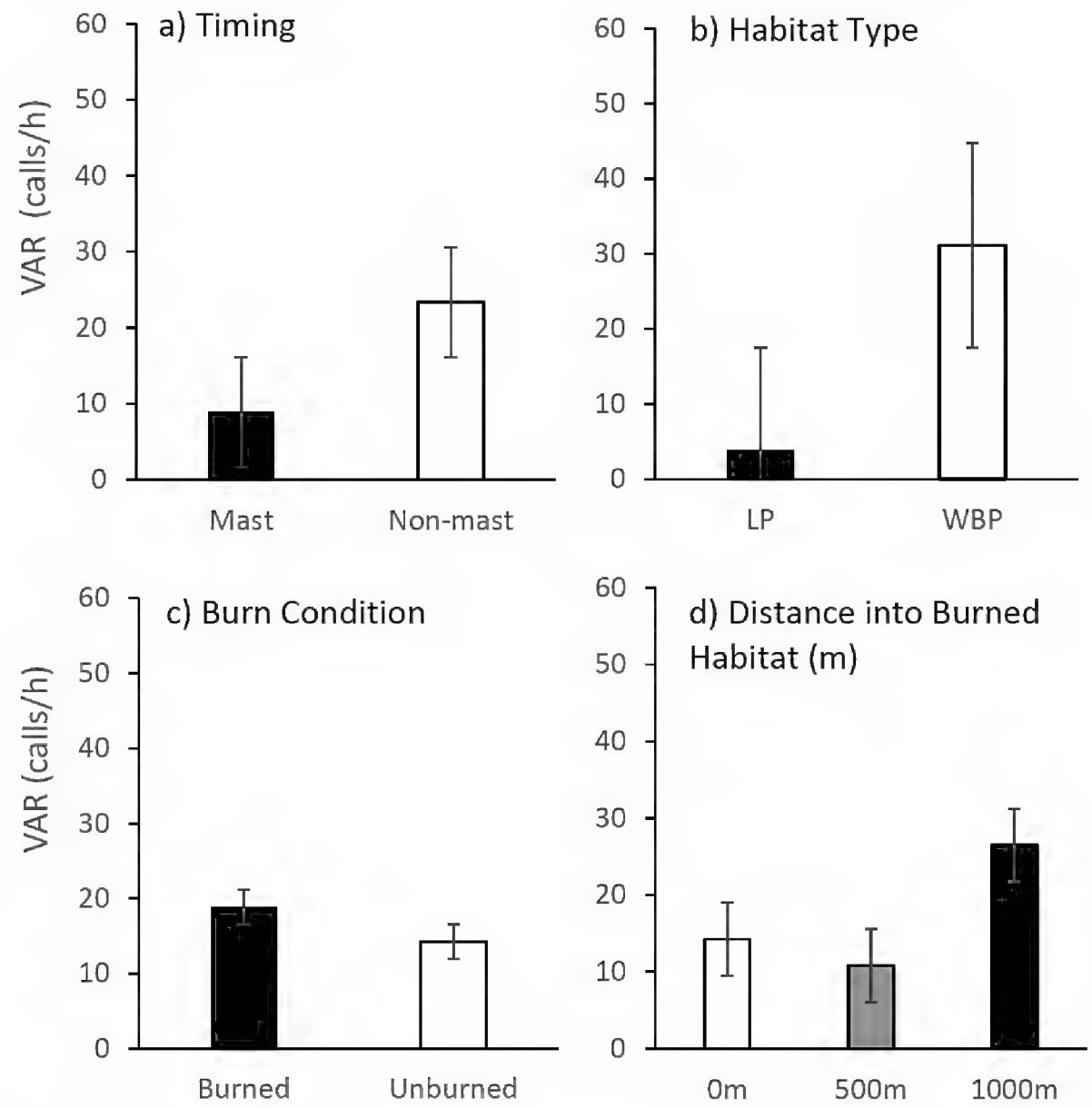

Figure 4. Nutcracker vocal activity rate (VAR) in the spring relative to seed availability and habitat factors. VAR is average nutcracker calls per hour (h) and is shown relative to: **a.** Mast versus non-mast year (n = 6 automatic recording units (ARU's), respectively); **b.** Limber pine (LP) versus whitebark pine (WBP) habitat (n = 3 ARU's, respectively); **c.** Burned versus unburned habitat (n = 4 and 2 ARU's, respectively); **d.** Distance into burned habitat (n = 2 ARU's, respectively), +/- 1 SE.

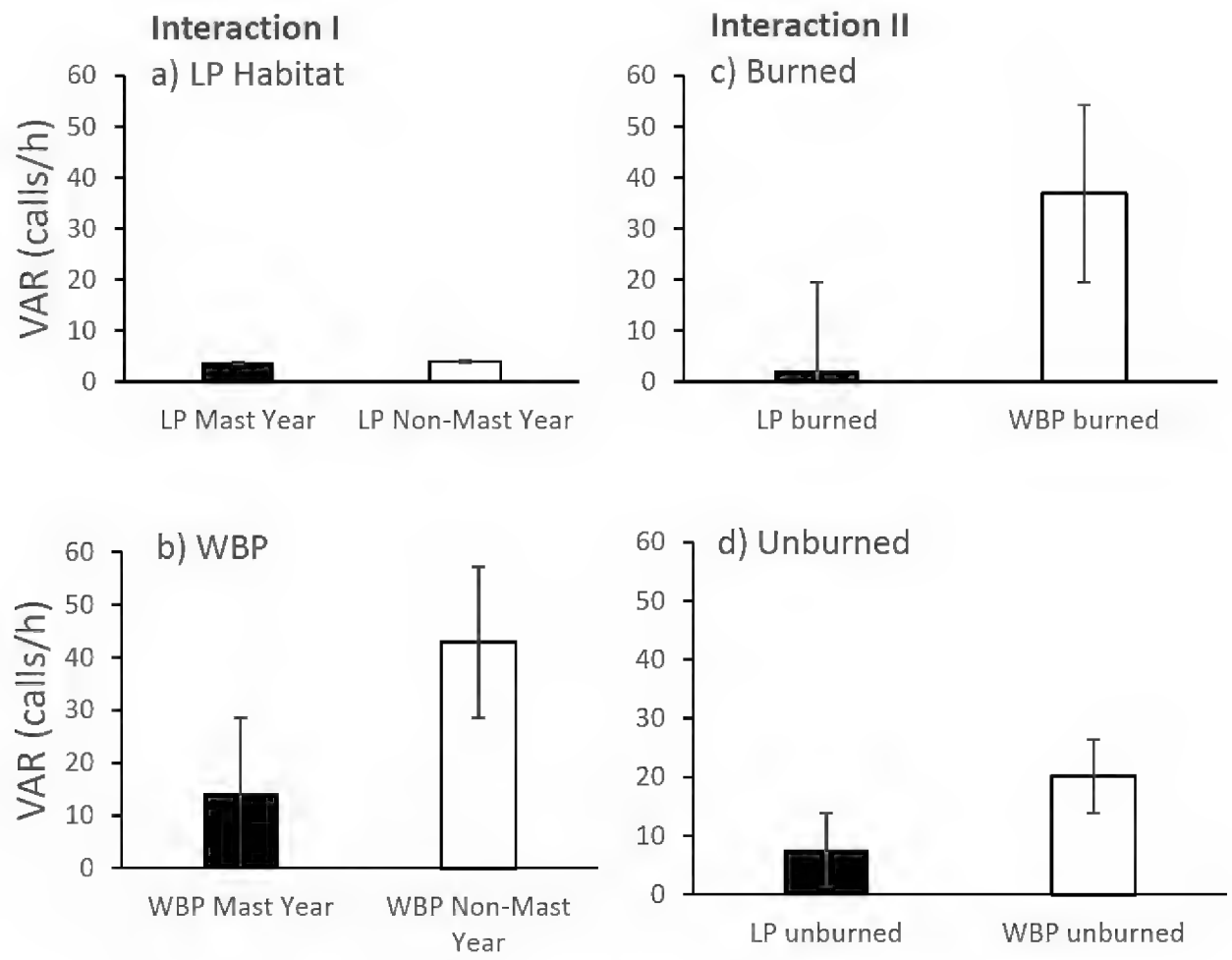

Figure 5. Nutcracker vocal activity rate (VAR) in the spring relative to habitat and seed availability interactions. VAR is average nutcracker calls per hour (h) and is depicted relative to interaction I, between habitat type (limber pine (LP) and whitebark pine (WBP)) and timing of mast versus non-mast year. Interaction 2 is between burn condition and habitat type. Standard error bars are shown (+/- 1 SE).

Discussion

Masting affects interannual habitat use by Clark's Nutcracker

Our results suggest that masting contributed to greater use of cone crops of both species by nutcrackers in the fall of the mast year (i.e. fall analysis), but that less use of both habitats occurred in the spring following the mast year (i.e. spring analysis). A growing number of studies have reported the attraction of nutcrackers to mast crops in the fall for several conifer species (Vander Wall 1988; Schaming 2016; Ray et al. 2020; Williams et al. 2020), although methodological differences in assessing cone crop metrics and nutcracker detectability, occurrence, or density, make direct comparisons difficult (Schaming et al. 2024). Clark's Nutcracker have been observed foraging on the cone crops of the species bearing the most abundant cones, transitioning to limber pine, Douglas-fir (*Pseudotsuga menziesii*), and ponderosa pine (*Pinus ponderosa*), in different years, according to their availability (Williams et al. 2020). Our results supported our prediction that Clark's Nutcrackers would be attracted locally to the studied burn in the fall foraging and caching season in a year with high cone availability of both limber and whitebark pine. The 2018 LP cone crop we studied exceeded all stand-level cone production measured in a province-wide mast event for LP in 2010 (n = 17 stands, and 680 trees in total). Although cones were also present in WBP in 2018, at a much lower density than LP, we are not aware of other studies in our region that assessed whether this was a regional masting event for WBP. Lower fall habitat use in the non-mast year may be explained if local birds left the areas in a year of cone failure, with long-distance irruptions, as reported in Vander Wall et al. (1981); however, long-distance irruptions have been linked to regional, multi-species cone crop failures and our data are limited to WBP and LP in one specific area. Temporal and spatial autocorrelation would be important analyses to consider in studies with longer temporal use data, and study sites spread over larger spatial scales. Such analyses could assess whether nutcrackers stay longer when mast crops are present, and what habitats they use, in the intervals between the fall and spring seasons that we studied.

A few studies have documented spring retrieval of seed caches in the field or documented breeding season habitat use (typically March to mid-June; Schaming 2016). Schaming (2016) found that nutcrackers selected WBP habitat more in spring following large cone crops, than in years of poor cone crops. Cached WBP seed was retrieved significantly more in years following a large WBP cone crop, than following a low cone crop year; however, cached seed retrieval represented only about 9% of the total foraging behavior documented (Schaming 2016). These findings occurred in Wyoming, in WBP habitats, with moderate to heavy tree mortality, in contrast to our study fire in a northern region where WBP and LP mortality is very low (Shepherd et al. 2018, and Peters et al. 2017, respectively) and cone production appears largely intact (*pers. obs.*). We expected greater nutcracker activity in the spring following the 2018 mast crop, to capitalize on cached seed from the previous year, but surprisingly, birds used 5-needle pine habitat more in the spring following a non-mast year. This may have created the potential for proportionately more seed cached in 2018 to escape retrieval by Clark's Nutcracker. Alternatively, birds may have retrieved seed more quickly after mast years, as has been observed amongst small mammals and mast crops in other pine species (Vander Wall 2002), and thus spent less

time foraging; however, this is speculative, and beyond the scope of our acoustic analyses of habitat use. A direct measurement of cached seed in 2018, and retrieved seed in 2019, and 2020 would be needed to test these hypotheses.

Several studies have hypothesized that masting would result in not only greater dispersal (Kelly 1994; Wall 2002), but even in regeneration (Hutchins and Lanner 1982). The fall dispersal and placement of seed in suitable regeneration microsites (i.e. caching) equals regeneration opportunity. The spring retrieval, and consumption of seed, means lost opportunities for regeneration. The relative balance of these two behaviours, along with granivory by rodents of cached seed (Lorenz et al. 2011), and germination success in relation to environmental factors, make it difficult to link regeneration to habitat use by Clark's Nutcracker without further research.

Avian seed dispersers are rarely satiated, except in systems where seed-bearing trees experience high seed predation (Janzen 1971; Herrera et al. 1998), as is the case in both LP and WBP which experience high rates of cone predation by red squirrels (McKinney and Fiedler 2009; Peters et al. 2017). Mast crops are known to allow a higher proportion of cones to escape red squirrels during active cone predation periods in July in LP (Peters et al. 2017), and WBP (Leslie and Wilson 2011), and prolong seed harvest in WBP (McKinney and Tomback 2007). Our mid-late August recording dates may have led to the collection of data from birds which were still able to forage successfully on available cones at this late date in the 2018 mast years, whereas in the 2019 non-mast years, these cones were likely removed by red squirrels by the end of July, based on predation dates reported by Leslie and Wilson (2011). Interestingly, there appeared to be less foraging in the spring retrieval period for WBP following mast years compared to LP habitat (1/3 the habitat use by Clark's nutcracker), which is difficult to compare to other studies of spring CLNU foraging, as both LP and WBP habitat were common in our system, but LP was rare in a comparable study (Schaming 2016). Seed removal from caches by mice and voles over the fall and winter of 2018–2019 could have influenced CLNU activity in the spring of 2019. Mice and voles have removed up to 90% of simulated WBP caches over fall and winter, although as noted by Lorenz et al. (2008), masting as a strategy by whitebark pine likely ensures seeds remain available for germination, suggesting high visitation in 2019 by CLNU is likely.

An important area of bioacoustic methods for 5-needle pine research is to test whether nutcracker calling and nutcracker caching and retrieval behavior are positively correlated. Our advanced classifier was trained with a dataset predominated by alarm and locational calls (90.5%), and some shrill/mew calls (9.5%), which likely influenced the sensitivity of calls detected in our analysis; however, it is beyond the scope of our research to link detected calls to foraging behaviors. Calling confirms that birds are present (Williams et al. 2020; Kovalenko et al. 2024), and VAR is commonly used as the metric of activity. However, calling does not mean that foraging activities are necessarily associated with calling. Individual birds that are in the act of caching seed or retrieving seed are actually silent; however, these activities are social activities, and other birds are frequently calling while these activities are occurring (Mewaldt 1956; Tomback et al. 2001a). In our focal behavior studies, we observed calling by some members of a group that coincided with silent seed caching and seed retrieval behaviors by other nearby birds,

in both the fall caching periods and spring seed retrieval periods studied. The groups studied were detected from point counts that spanned several km of intervening LP and WBP habitat between ARU's. Locating birds was difficult, and neither our FBS nor our acoustic monitoring would detect lone birds that could silently harvest seeds and cache them or retrieve them.

Nutcrackers used WBP habitat more than LP habitat

Nutcrackers are known to cache in many forest types (Goeking et al. 2019) and given the wide variation in stand characteristics across the distribution of both pine species, there may be many factors driving nutcracker habitat use. Schaming et al. (2024) reports widespread use of both WBP and LP by nutcrackers across the pines' geographical distribution. In our study near the northern limits of both pine species, their co-occurrence on the same burn (separated only by elevation), provided a good test case of nutcracker habitat use when cones were available and seed retrieval was probable. Nutcrackers preferred WBP habitat over LP habitat during both the fall (1.3 times greater) and the spring (7.1 times greater), showing strong preference for burned WBP vs. burned LP habitat in the spring (15.7 times greater). This occurred despite far more LP cone availability than WBP (12 times greater cones/tree, and 10.5 times greater BA in LP than WBP, respectively; Table 1). Nutcrackers have been observed to select WBP cones in a probabilistic manner as cone densities increase, with an 83% likelihood of occurrence at 1000 cones per ha, which required a basal area of 5 m^2/ha (McKinney et al. 2009). Further, recent bioacoustic analyses have been paired with point counts to show nutcrackers show greater occupancy and vocalization activity in WBP stands with high cone densities and larger stem diameters (Kovalenko et al. 2024). We observed considerable fall visitation by Clark's Nutcracker (100% of days) in our unburned WBP stands at much lower basal areas (0.2 m^2/ha) in 2018, and likely fewer cones per ha. Our WBP had widely spaced mature trees, and many immature trees that had not reached cone bearing age. Several studies have also reported visitation at low cone densities (Barringer et al. 2012; Kovalenko et al. 2024). In our study, there was an apparent preference for WBP habitat that occurred in a landscape context where LP stands effectively escape cone predation by squirrels in mast years (58% of cones remain on average; Peters et al. 2017), and caching could potentially satiate post-dispersal seed predators. Compared to WBP, LP is less dependent on nutcrackers for seed dispersal because its cones open during seed ripening and opportunities exist for seed dispersal by barochory (gravity-dispersal) and granivorous animals (Tomback et al. 2005; Lorenz et al. 2011).

Nutcrackers forage on a wide variety of conifer species (Vander Wall 1988; Schaming 2016), however, they may prefer certain species over others for site-specific reasons, including proximity of cone trees to caching sites, nesting areas, snow cover, and protective cover during foraging and caching (Schaming 2015; Schaming 2016). Monitoring of fall habitat use coincided with periods when foraging, caching, or pouching had previously been observed in both LP (Vander Wall 1988) and WBP (Leslie and Wilson 2011; Scott 2013; Schaming et al. 2024). Prior studies suggest that nutcrackers show an elevational migration associated with cone maturation, ascending from LP to WBP habitat as

cones mature. Nesting habitat has been observed across a range of elevations (Tomback 1998). Preference for WBP habitat in our study may have positioned nutcrackers closer to nesting habitat. Our WBP site 1000 m into the burn occurred near a large, unburned stand of lodgepole pine (*Pinus contorta*) within the burn perimeter, where nutcrackers were observed to be nesting; similar nesting habitat was also available near the unburned WBP seed source. The timing of spring recordings (May 20th – June 16th), may have favored WBP habitat use as newly exposed caching sites increased in availability, particularly in burned areas. Nutcrackers may have retrieved seed earlier in LP, owing to their occurrence at lower elevations; and earlier exposure of caching sites. We can only speculate on these effects, as sampling coincided with a time when upper elevation WBP sites were first exposed by snow retreat.

Effect of burned habitat on nutcracker activity

Vocal activity patterns switched from higher use of unburned habitat in the fall, to proportionately higher use in burned areas in the spring. A possible explanation for the seasonal difference is the simple fact that nutcrackers both collect seed and cache seed in unburned seed source stands in the fall, thereby increasing activity time there, versus engaging solely in caching activity in the burn. Equal or greater seedling regeneration in unburned stands than within burns for WBP and LP, on this fire, and more broadly throughout the northern distribution of the pines, demonstrates the extent of caching within unburned seed sources (Gelderman et al. 2016; Salvador 2018; Dawe et al. 2019; Peters and Visscher 2019). Nutcrackers have been documented to prefer caching under canopy cover in unburned areas. They may prefer this for many reasons, including: caching seeds close to a seed source requires less energy than caching farther away, coverage from unburned trees provides a visual barrier from predators (Lorenz et al. 2011; Dawe et al. 2019), and how they use spatial memory to locate caches, and feed young during nesting, incubating, and chick rearing time periods.

Our burned habitat appeared to be seral WBP and lodgepole pine mixtures, and seral limber pine and lodgepole pine, with abundant lodgepole pine regeneration (Salvador 2018; Dawe et al. 2019). Unburned habitat may be as important, if not more important, for sustained regeneration, particularly for LP, where canopies remained open (Dawe et al. 2019; Peters and Visscher 2019). Environmental variation occurred across the burn, and surrounding unburned stands, likely creating the conditions where patchy seral communities and sites that are self-regenerating could result (Tomback and Achuff 2010).

Limitations to acoustic analyses

One limitation of our study was the inability to examine the effect of weather or elevation on calling, because the reliability of the advanced classifier in detecting nutcrackers correctly depends on removing recordings with high interference from wind, rain, or other background noise. Analyses of the distribution of recordings removed indicated that there were no significant associations between any of the factors tested in spring or fall models. Overall, these results suggest that weather did not disproportionately affect the number of usable versus omitted recordings. A sample of recordings for high sound inter-

ference also showed some of the highest interference in mid-elevation (WBP 1000 m from wind and rain), and low elevations (LP 0 m from vehicle traffic), suggesting other factors could affect individuals ARUs.

Nutcracker habitat use and regeneration patterns at the northern range limit

We undertook this study to not only address broadly applicable knowledge gaps in nutcracker habitat use, but to try to understand the regeneration process of both pine species at their northern range limit, where managers intentionally conducted the 2009 prescribed burn in this study to facilitate seed dispersal and regeneration. The lack of LP regeneration on two recent burns (2001 and 2009), in contrast to successful WBP regeneration (6.3 seedling clusters/ha versus 206 seedlings/ha, respectively), raised questions about whether nutcrackers were dispersing both species effectively (Salvador 2018; Dawe et al. 2019; AEP 2022). We recognize that the nutcracker activity we studied would result in future seedlings, not documented in the current study. Documenting the current activity of nutcrackers shows whether nutcrackers relate to habitats where regeneration is occurring differently from habitats where regeneration is not occurring. Such regeneration patterns could arise if nutcrackers displayed a preference for WBP habitat over LP habitat on burns during fall dispersal, or spent more time in LP habitat during the spring retrieval period. The latter prediction did not occur in the period we studied, and it appeared that nutcrackers would be more likely to limit WBP regeneration than LP on burns, through cache retrieval. It is important to note that direct measurement of cache retrieval is required to test this hypothesis and was beyond the scope of our study. Additionally, a combination of other ecological factors affect germination and seedling survival, as LP occurs on more arid sites than WBP on the burn, and experiences a longer snow-free period, pre-disposing it to longer periods of seed retrieval by other nutcrackers, or mammalian seed predators.

Fire management and recovery plans

Further study of nutcracker and 5-needled pine regeneration is warranted throughout the distribution of both pines, in the variety of stand types, and fire regimes that occur. In Alberta, our study burn represented one of the few known locations where both pine species co-occur, and the only burn, in addition to three wildfires, known to have occurred in LP habitat in the last 40 years. Several times more wildfires and prescribed burns have occurred in WBP habitat in the province in the same period, with successful WBP regeneration at greater than 20 years post-fire (Moody 2006). Our results can inform the development of more detailed studies on nutcracker habitat use, and reducing uncertainty in the factors that drive postfire regeneration dynamics in LP and WBP.

At a broader scale of fire management and 5-needle pine recovery, the availability of burned sites is expected to increase in Canada with climate change (Gillett et al. 2004), allowing for potential future natural regeneration opportunities. More importantly, the continued use of white pine blister rust resistant trees by dispersers is essential for natural regeneration to be effective in current recovery strategies. If this occurs, fires could provide opportunities for building resilient populations to white pine blister rust. Understanding Clark's

Nutcracker habitat use is important for studies modeling the success of restoration plantings as focal points for population growth; once resistant seedlings reach cone bearing age, Clark's Nutcracker seed dispersal can leverage current restoration efforts. Fire management goals will likely differ between ecoregions in Canada and the US; however, the ongoing considerations of stand characteristics and openness are warranted (Retzlaff et al. 2018).

Conclusions

The seed dispersal mutualism between Clark's Nutcracker and some 5-needled pines is evidenced in the two key seasonal behaviors of fall seed caching and seed retrieval, which exert individual effects on the regeneration process. At the northern range limits of where LP and WBP co-occur, acoustic analyses demonstrated that nutcrackers used WBP habitat more than LP habitat across season (fall and spring), and cone supply (mast vs. non-mast year). Models of fall habitat use by Clark's Nutcracker identified positive effects from masting, and unburned stand condition across both LP and WBP habitat. Spring retrieval models showed increased differences between LP and WBP habitat, where nutcrackers targeted burned WBP habitat. Our results provide information on temporal variation in habitat use on a single large burn, highlighting the need for studies of Clark's Nutcracker habitat use in other parts of WBP and LP geographic range. Habitat use information is essential to inform recovery plans on potential for natural dispersal and regeneration in 5-needle pine habitat where wildfire is likely, and white pine blister rust resistant trees are abundant. Field validation of acoustic analysis linked to Clark's Nutcracker behavior is needed to quantify the nutcracker's role in seed dispersal and seed retrieval so that their effect on seed availability and regeneration can be understood. Future research could do well to link VAR to natural regeneration success of LP and WBP across their distribution to identify locations where each species will benefit more from supplemental planting of disease-resistant seedlings.

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Additional information

Conflict of interest

The authors declare no known competing financial or personal interest that could appear to influence the research reported here. The funders had no role in the design, data collection, analyses, or interpretation of results, manuscript preparation, or publishing decisions.

Ethical statement

Animals in science: Passive monitoring technologies for bird activity in this study followed the "3 R" strategy in EU legislation, specifically, the "Replacement" principle, and complied with relevant laws, and institutional guidelines that follow the NSERC and SHERC policies, and institutional committee requirements.

Use of AI

The authors accept full responsibility for the content of the manuscript, including the disclosure of any use of AI. No AI tools were used in the preparation of this manuscript.

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Author contributions

V.S.P. conceived, designed, acquired funding, administered, and supervised the study. V.S.P., J.V., K.G., E.B., and C.E.P. collected, and analyzed the acoustic data. D.P. designed the acoustic monitoring approach, and reviewed and edited the paper. J.V. conducted the statistical analysis, and wrote the original draft. J.V. and C.E.P. edited the paper. V.S.P wrote the submitted manuscript, and edited the paper.

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Data availability

All of the data that support the findings of this study are available in the main text.

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Appendix 1

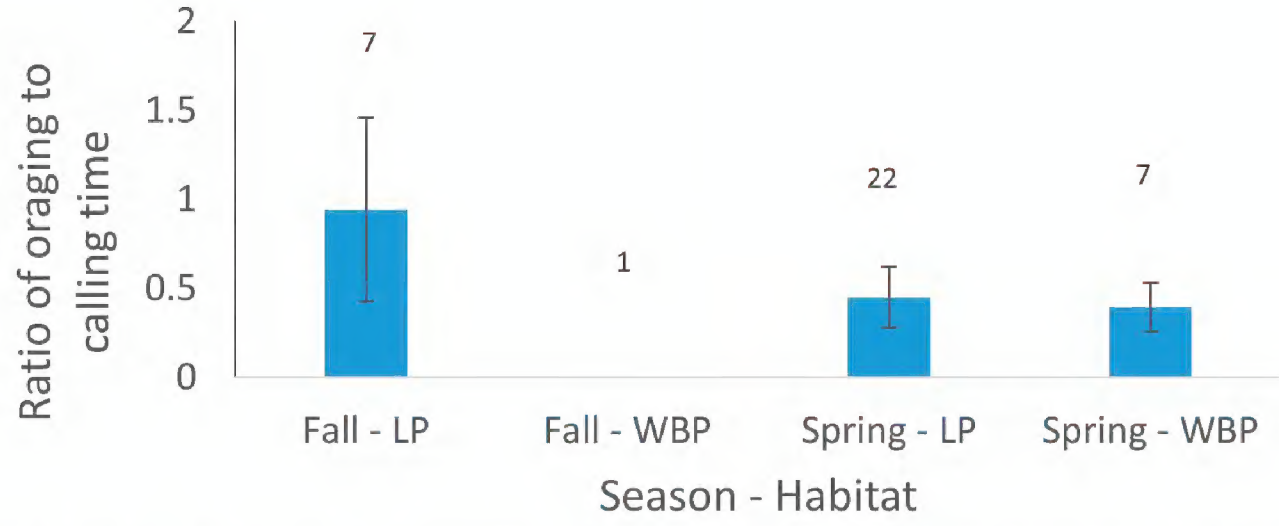

Figure A1. The ratio of foraging time, relative to calling time in focal behaviour studies. Fall and spring foraging behavior (caching and seed retrieval, respectively), is shown in limber (LP) and whitebark pine habitat (WBP), respectively. Note, foraging individuals were typically quiet, while other birds in the same group called. The number of focal behavior studies per sampling period is shown above the vertical bars, and +/- 1 SE is shown for each ratio. Inclement weather prevented the collection of more fall WBP studies.